Nervous System and Musculature of Pregenital Abdominal Segments of Male Stonefly Nymph, *Acroneuria* (Plecoptera: Perlidae)*

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Abstract The nervous system of the pregenital abdominal segments of the male nymph of *Acroneuria* sp. is described. The ganglia of the first two abdominal segments are coalesced with the metathoracic ganglion. The transverse nerve in segments 2 through 8 arises from the ganglion with the dorsal nerve, splits off in the area of the ventral internal lateral muscles, and terminates in the alary muscles of the heart. Ventral nerves are present in all segments. The musculature of the pregenital segments is described.

The order Plecoptera is often referred to as being orthopteroid, or closely related to the Orthoptera in origin. In his study of the nervous system of the abdomen of the stonefly *Pteronarcys*, a genus considered to be generalized, Schmitt (1963), noted that the complex genitalia, reduced musculature, and the unusual transverse nerve arrangement seem far removed from the arrangement of these structures in the abdomen of the Orthoptera. Schmitt's study pointed out the need for more knowledge about the abdominal morphology of other Plecoptera, so that the origin of abdominal structures in this order might be better understood.

It was for this purpose that the present study of the abdominal nervous system of *Acroneuria* was undertaken. This genus, in the family Perlidae (whose members are small, flattened, and carnivorous), was selected as being a suitable contrast to the large herbivorous *Pteronarcys*. The present study includes the muscles and nerves of the pregenital abdominal segments of the male nymph.

MATERIALS AND METHODS

Male nymphs were selected for study because the egg masses and fat body in the abdomen of the female nymphs distorted structures and made dissection difficult. The nymphs were collected from a stream in Mountain Lakes, New Jersey, with the help of Dr. Lyle E. Hagmann.

Nymphs were either injected with formaldehyde–alcohol–acetic acid fixative (F.A.A.) in the field or brought back to the laboratory live in damp gauze. Dissections were performed on preserved nymphs, on live nymphs in isotonic salt solution, and on live nymphs which had been injected with methylene blue chloride.

RESULTS

Pregenital musculature of male nymph

The abdominal musculature of the male nymph of *Acroneuria* conforms quite

* Paper of the Journal Series, N. J. Agric. Exp. Sta., Rutgers—The State University, Dept. of Ent. and Economic Zool.

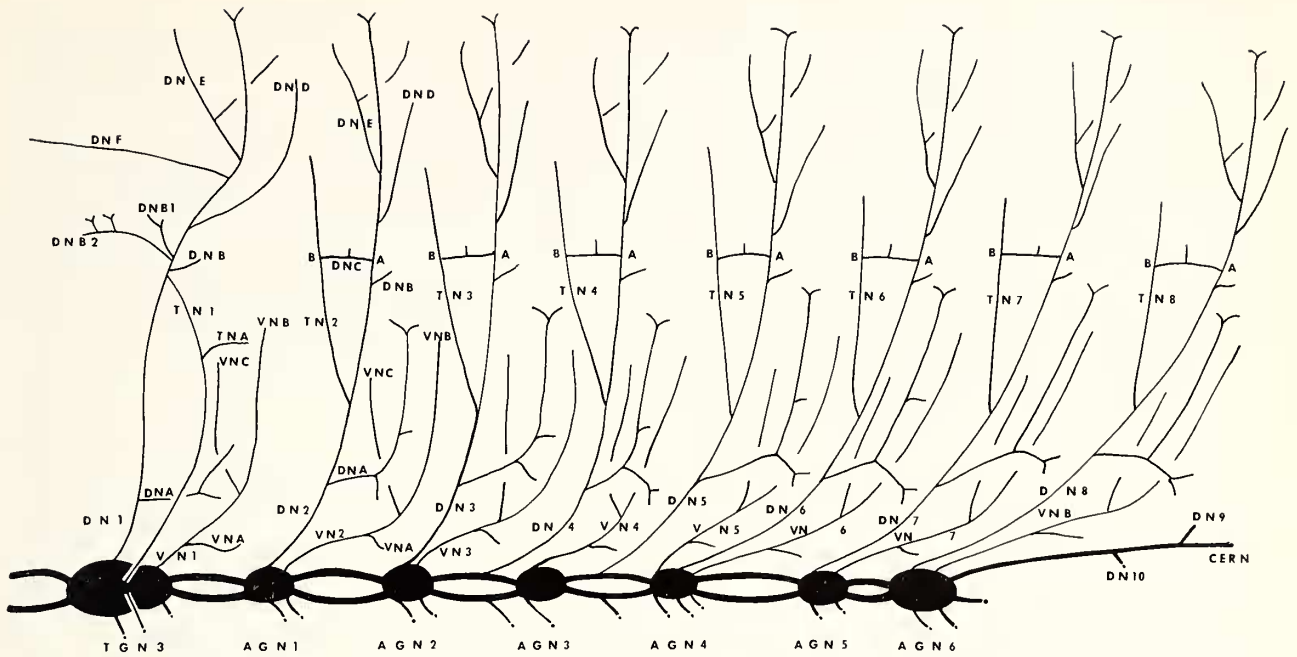

Fig. 1. Nerves of pregenital abdominal segments of *Acroneuria*, right side.

closely to that found by Maki (1938), Ford (1923), and Wittig (1955) in other members of the Perlidae.

Fig. 2A shows the muscles of the right half of the pregenital abdomen of *Acroneuria*. (I have followed Snodgrass (1935) in naming the abdominal muscles. The predominant muscles are the internal longitudinal muscles.)

The ventral longitudinal muscles (See Fig. 2A) are present in two groups: the ventral internal muscles (VIM) and the ventral external muscles (VEM). The fibers of the ventral internal muscles extend in each segment from one intersegmental ridge to another and are present in three groups. The two median groups, which are external to the dorsal nerves and closest to the ventral nerve cord, are termed the ventral internal median muscles (VIMM). The third group is located internal to the dorsal nerve, lateral of the ventral internal median muscles, and is termed the ventral internal lateral muscle (VILM). The ventral internal muscles of the first abdominal segment are continuous with the ventral internal muscles of the third thoracic segment. The ventral external muscles in each segment arise on the sternum and insert on the posterior intersegmental ridge of the segment. In each segment one muscle is located close to the nerve cord, external to the ventral internal median muscles; it is termed the ventral external median muscles (VEMM). The other muscle, located laterally external to the ventral internal lateral muscles, is termed the ventral external lateral muscle (VELM).

There are two main groups of dorsal muscles: the dorsal internal muscles (DIM) and the dorsal external muscles (DEM). The dorsal internal muscles (See Fig. 2A) are powerful bands of muscles, extending from one intersegmental ridge to the next in the dorsal half of the abdomen, divided on the middorsal line by the heart. On each side of the heart they are divided into four longi-

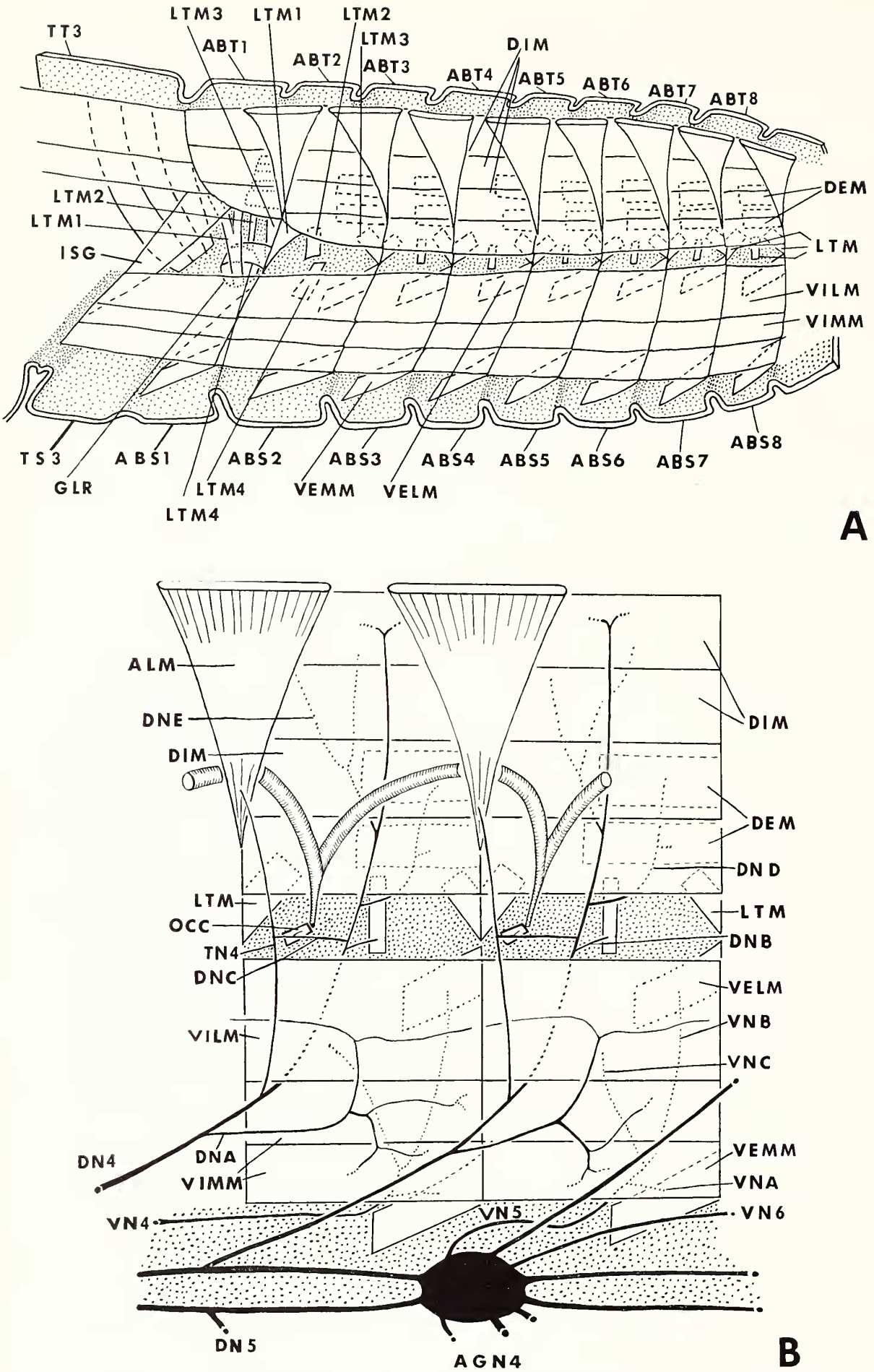

FIG. 2. *Acroneuria* A. Musculature of pregenital abdominal segments, right side. B. Musculature and nerves of the fourth and fifth abdominal segments, right side.

tudinal bands of fibers. In the first segment there are three bands of muscle on each side. The dorsal external muscles are very small bands of muscle arising on the middle of the dorsum of each segment and inserting on the posterior intersegmental ridge, external to the dorsal internal muscles.

The ventral diaphragm is absent. The muscles of the dorsal diaphragm are the alary muscles of the heart (ALM). They arise on the intersegmental ridges, fan out, and insert on the wall of the heart.

Except in the first abdominal segment the lateral muscles are much reduced (See Fig. 2A). In each lateral half of the second abdominal segment there are three tergosternal muscles (LTM 1, 2, 3) and one sternopleural muscle (LTM 4). In each lateral half of segments three through eight there are three tergosternal muscles. The muscles of the first abdominal segment are intimately connected with those of the metathorax. In each lateral half of the segment one large intersegmental muscle (ISG) extends from the intersegmental ridge of the metathorax to the dorsum of the first abdominal segment. There are four intergosternal muscles in each half of the segment. Two (LTM 1, 2) arise on the dorsum and insert on the gill ridge. Another (LTM 3) arises on the dorsum and inserts on the gill ridge. Another (LTM 3) arises on the dorsum and inserts on the intersegmental ridge between the first and second segments. Another muscle (LTM 4) arises on the same ridge and inserts on the gill ridge. A small occlusor of the spiracle (OCC) is present in segments two through eight.

Abdominal nervous system

The abdominal nerve cord of *Acroneuria* contains six definitive ganglia (Fig. 1). The ganglionic centers of the first two abdominal segments are contained in the metathoracic ganglion. The first definitive abdominal ganglion contains the ganglionic center for the third abdominal segment, the second abdominal ganglion serves the fourth segment, and the third ganglion serves the fifth segment. The fourth ganglion serves the sixth segment, and the fifth ganglion serves the seventh segment. The sixth ganglion supplies nerves to the eighth, ninth, and tenth segments, as well as to the cerci. The abdominal nerve cord extends posteriorly in a midventral position. The first abdominal ganglion is located midventrally in the first abdominal segment. The second ganglion is also located in the first segment, while the third is located between the second and third segments. The fourth is located anteriorly in the fifth segment; the fifth is located in the sixth segment and the sixth in the seventh segment.

In naming the segmental nerves, I have followed Schmitt (1954, 1962, 1963) since his terminology seems to have the greatest morphological significance. Only the nerves of the right half of the abdomen are shown in the diagrams (Figs. 1 and 2).

The dorsal nerve of the first abdominal segment, dorsal nerve one (DN 1), arises from the metathoracic ganglion and passes laterally internal to the ventral internal median muscles (Fig. 1). A branch from dorsal nerve one, dorsal nerve

A (DN A), innervates the ventral internal median muscles. Dorsal nerve one then passes external to the ventral internal lateral muscles. Several branches (DN B, DNB 1, and DNB 2) innervate the lateral muscles and the large intersegmental muscle. Dorsal nerve one then passes dorsally to innervate the dorsal muscles. A branch, dorsal nerve D (DN D), passes external to the dorsal internal muscles and innervates the dorsal external muscles. After meeting the dorsal internal muscles the dorsal nerve gives off a branch (DN F) which passes anteriorly to join with the nerve which innervates the dorsal longitudinal muscles of the metathorax. The dorsal nerve then proceeds dorsally, innervating the dorsal internal muscles and giving off a branch, dorsal nerve E (DN E) which travels externally through the dorsal muscles and innervates the dorsal integument. The ventral nerve (See Fig. 1) of the first abdominal segment (VN 1) arises from the metathoracic ganglion and passes external to the ventral internal median muscles. One branch (VN A) innervates the ventral median external muscles; the ventral nerve then bifurcates, one branch (VN B) innervating the lateral external muscles, while the other branch (VN C) innervates the ventral integument. The transverse nerve of the first abdominal segment arises from the middorsal surface of the metathoracic ganglion and passes internal to the ventral muscles, giving off a branch (TN A) which innervates the ventral internal lateral muscles. In the area of the lateral muscles it joins with the dorsal nerve.

The dorsal nerve of the second abdominal segment, dorsal nerve two (DN 2), arises from the anterior end of the first abdominal ganglion (See Fig. 1). In stained specimens the fibers of this nerve, and of the ventral nerve of this segment, can be seen to pass through the interganglionic connective to the metathoracic ganglion. It is assumed, therefore, that the ganglionic center for this segment is contained in the metathoracic ganglion. Dorsal nerve two passes laterally internal to the ventral internal median muscles, giving off a branch (DN A) which innervates both the ventral internal median and lateral muscles. It then gives off a branch which travels dorsally internal to the ventral internal lateral muscles and innervates the alary muscle which is inserted on the intersegmental ridge between the first and second abdominal segments. This branch is termed transverse nerve two (TN 2). It is called the transverse nerve for three reasons: one, such an arrangement of the transverse nerve (where the transverse nerve arises from the ganglion with the dorsal nerve) is found in the posterior segments of *Pteronarcys* (Schmitt, 1963); two, this nerve innervates the transverse muscles (the dorsal alary muscles); and three, as found with the transverse nerve in Orthoptera and *Pteronarcys*, there is a connection between this nerve and the dorsal nerve, termed "the A–B connection" by Schmitt. After the transverse nerve has branched off, the dorsal nerve passes external to the ventral internal lateral muscles. A small branch, dorsal nerve B (DN B), innervates one of the tergosternal muscles. In the area

of the spiracle a small branch (DN C) arises from the dorsal nerve which joins with the transverse nerve of this segment. This connecting branch seems to be homologous with the A–B connection between the transverse and dorsal nerves found by Schmitt (1963) in *Pteronarcys*. From this connecting branch arises the innervation of the occlusor of the spiracle. Dorsal nerve two then travels dorsally to the dorsal muscles, giving off a branch, dorsal nerve D (DN D), which innervates the dorsal external muscles. The dorsal nerve continues dorsally innervating the dorsal internal muscles and giving off a small branch (DN E) which travels through the dorsal muscles to the integument, and bifurcates and innervates the dorsal integument.

The ventral nerve of the second segment (VN 2) travels posteriorly along the nerve cord to the second segment (Fig. 1); it then passes laterally external to the ventral internal muscles. It gives off a short branch to the ventral external median muscles (VN A), then bifurcates, one branch (VN B) innervating the ventral external lateral muscles and the sternopleural muscle and the other branch (VN C) the ventral integument.

The pattern of innervation in segments three through eight is the same as in segment two as shown in Figs. 1 and 2B. The dorsal nerve provides the innervation for the dorsal longitudinal muscles, the dorsal integument, and the ventral internal longitudinal muscles. The transverse nerve innervates the alary muscles and from the connecting nerve (DN C) between the dorsal and transverse nerves arises the innervation for the occlusor of the spiracle. The ventral nerve innervates the ventral external muscles and the ventral integument.

DISCUSSION

In order to homologize nervous systems of various insects it is necessary to identify anatomical similarities. The dorsal nerve can be recognized by its innervation of the dorsal musculature. Where there has been fusion of nerves, the combination of nerves often can be identified by the muscles innervated. The anatomical makeup of the nervous system is useful in determining morphological relationships.

One of the best examples of this is the connection between the dorsal nerve and the transverse nerve as found in the abdomen in Orthoptera and Plecoptera by Schmitt (1954, 1962, 1963) and in Lepidoptera by Libby (1959). This nerve connection, dorsal nerve C (also termed the A–B connection by Schmitt, Libby, and the present author), occurs in the area of the spiracle and gives rise to the innervation of the spiracular muscles when they are present (Fig. 2B). This same nerve loop is recorded by Maki (1936) in the alder fly. According to Schmitt (1962) the occurrence of this nerve loop in such widely separate groups makes it very useful in considering morphological relationships.

As might be expected in insects which exploit very different habitats, there

are distinct differences to be found between *Acroneuria* and the Orthoptera. The muscles of the Orthoptera abdomen are arranged so that they perform efficiently the powerful ventilation movements of the abdomen, which aerate the tracheal system. The lateral muscles, important in these movements, are large and powerful. The muscles of the abdomen of Orthoptera are not important in locomotive movements. Just the opposite is true in the plecopteran nymph. The longitudinal (internal) muscles are responsible for the swimming movements of the abdomen and are large and powerful. The lateral abdominal muscles perform no ventilation movements in this aquatic insect, and these muscles, correspondingly, are tiny and almost nonfunctional.

The A–B connection between the transverse nerve and the dorsal nerve is present in the Orthoptera and the Plecoptera; however, neither in *Acroneuria* nor in *Pteronarcys* is there any connection between the ventral nerve and the dorsal nerve as there is in the Orthoptera.

Schmitt, in his study of the abdomen of *Pteronarcys* (1963) noted the strange fact that in several segments the apparent ganglionic origin of the transverse nerve is from the ganglion posterior to the ganglion in which the dorsal nerve for that segment arises. One of the purposes of the present study was to determine if this strange arrangement occurs in another member of the Plecoptera. In *Acroneuria* no trace of any such arrangement was found. No median nerve was present and, except in the first segment, the fibers of the transverse nerve arise from the ganglion with the fibers of the dorsal nerve. This same arrangement was found by Schmitt in the posterior segments of *Pteronarcys*. In *Acroneuria* there was more forward migration of ganglionic centers than in *Pteronarcys*, and there was no atrophy of the ventral nerve or the ventral external muscles. This would indicate that these two families have diverged greatly in their evolution.

Studies on the nervous systems of the abdomens of widely separated groups have done much to indicate that there is a basic segmental abdominal nerve plan which can be recognized even in very specialized insects. In Lepidoptera, Orthoptera, Neuroptera, and Plecoptera the dorsal nerve innervates quite regularly the dorsal muscles and integument and the ventral internal muscles. The ventral nerve innervates the ventral external muscles and the ventral integument. Perhaps most important, the A–B connection between the dorsal and transverse nerves is present in all of these orders, indicating that this is an important landmark and a characteristic of a basic segmental nerve plan. A connection between the ventral nerve and the tranverse nerve found by Schmitt (1954) in some Orthoptera and by Libby (1959) in Lepidoptera (the cecropia moth) was not found in *Acroneuria* or in *Pteronarcys* (Schmitt, 1963).

The results of this study agree well with the hypothesis that a basic segmental nerve plan exists. Only more and varied studies of the insect nervous system can indicate how wide is the application of this generalization.

SUMMARY

The basic muscle pattern of a typical pregenital abdominal segment of *Acroneuria* includes the following muscles: dorsal internal muscles, dorsal external muscles, ventral internal muscles, ventral external muscles, three lateral muscles, dorsal transverse muscles, and an occlusor of the spiracle.

The innervation of a typical pregenital abdominal segment of *Acroneuria* is supplied by three nerves: a dorsal nerve which innervates the dorsal muscles, the dorsal integument, the ventral internal muscles, and the lateral muscles; a ventral nerve which innervates the ventral external muscles and the ventral integument; a transverse nerve, arising from the nerve cord with the dorsal nerve, separating in the area of the ventral internal lateral muscles, innervating the dorsal transverse or alary muscles, and, in the area of the spiracle, being connected to the dorsal nerve by a short branch (DN C).

An important landmark discussed by Schmitt (1962), the A–B connection between the dorsal nerve and the transverse nerve, was found in *Acroneuria*. This connection between the dorsal and transverse nerves was found in various Orthoptera by Schmitt (1954), in Neuroptera by Maki (1936) and Hammar (1908), in Lepidoptera by Libby (1959), and in Plecoptera by Schmitt (1963).

Similarities of muscle innervation by the various segmental nerves in the abdomens of various insects and the widespread occurrence of the A–B connection indicate the presence of a basic segmental nerve plan in insects.

ABBREVIATIONS USED ON THE FIGURES

A–B	connection between the dorsal and transverse nerves
ABS 1 to 8	abdominal sterna
ABT 1 to 9	abdominal terga
AGN 1 to 6	definitive abdominal ganglia
ALM	alary muscle
CERN	cercus nerve
DEM	dorsal external muscle
DIM	dorsal internal muscle
DN A to F	branches of the dorsal nerve
DN 1 to 10	dorsal nerve roots
GLR	gill ridge
ISG	intersegmental muscle
LTM 1 to 4	lateral muscles (tergosternal and tergopleural)
OCC	occlusor muscle of the spiracle
TGN 3	thoracic ganglion three
TN	transverse nerve
TS 3	metathoracic sternum
TT 3	metathoracic tergum
VELM	ventral external lateral muscle
VEMM	ventral external median muscle
VILM	ventral internal lateral muscle
VIMM	ventral internal median muscle
VN A to C	branches of the ventral nerve
VN 1 to 8	ventral nerve roots

Acknowledgments The author wishes to express her gratitude to Dr. J. B. Schmitt for his helpful suggestions during the course of this work and in the preparation of this paper, and to Dr. L. E. Hagmann for his suggestions concerning staining and histological work.

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RECEIVED FOR PUBLICATION JANUARY 5, 1965